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# MULTIPLE PATTERNS OF DEVELOPMENT IN *STREBLOSPIO BENEDICTI* WEBSTER (SPIONIDAE) FROM THREE COASTS OF NORTH AMERICA

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## ABSTRACT

*Streblospio benedicti* Webster, a small tube-dwelling polychaete common in Pacific, Gulf of Mexico, and Atlantic estuaries of North America, exhibits both lecithotrophic and planktotrophic modes of larval development. In lecithotrophic forms females produce few (9–50) large ova (100–200 $\mu$m diam.). These develop in dorsal pouches into 9–12 setiger larvae, competent to settle at release. Females of planktotrophic forms produce large broods (100–548) of small ova (70–90 $\mu$m), brood larvae in dorsal pouches or beneath dorsal branchiae, and release 3–7 setiger larvae which bear long swimming setae and feed in the plankton for 1–5 weeks before settling. Lecithotrophy is reported for *S. benedicti* populations on all three coasts of N. America, planktotrophy from the Atlantic and Gulf coasts only. Reproductive differences observed in the field are maintained by laboratory cultures reared under constant (20°C) conditions, though individuals from planktotrophic and lecithotrophic populations are interfertile. Developmental variations observed in the field are believed to generate different patterns of dispersal, recruitment, population growth (r), and mortality. Poicilogony, the occurrence of multiple development modes, may account for the considerable success of *S. benedicti* in N. America.

## INTRODUCTION

This paper describes the occurrence of both planktotrophic (feeding) and lecithotrophic (non-feeding) modes of development in the estuarine polychaete *Streblospio benedicti*. The dichotomy between these development modes in marine invertebrates, and between associated variations in egg size, fecundity, and length of planktonic larval life, have generated interest among developmental biologists, zoologists, and ecologists for many years (Thorson, 1946, 1950). These traits and their ecological implications are examined here for a single species.

The adaptive nature of marine invertebrate trophic modes remains a mystery despite theoretical efforts to model the coexistence of reproductive strategies (Vance, 1973a, b; Christiansen and Fenchel, 1979; Pechenik, 1979; Caswell, 1981) and an empirical search for energetic correlates of alternate development patterns (Hines, 1979; Spight, 1979; Todd, 1979; Hughes and Roberts, 1980; Grahame, 1982; Defreese and Clark, 1983). Clues to the adaptive differences between planktotrophy and lecithotrophy may be found in the study of poicilogonous species, those species which exhibit multiple reproductive modes. Such variability is especially common among the Spionidae (Polychaeta), in which brood protection and nurse egg feeding (adelphophagy) allow considerable flexibility in the duration of the planktonic larval phase and in the mode of nutrition. Multiple patterns of larval development have been

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described in *Pygospio elegens* (Rasmussen, 1973), *Spio setosa* (Simon, 1968), *Polydora quadrilobata* (Blake, 1969), and *Boccardia proboscidea* (Blake and Kudenov, 1981). However, none of these investigations has shown a single female to produce both planktotrophic and lecithotrophic (non adelphophagic) larvae, and crossing experiments have not been conducted to eliminate the possibility of speciation. In several instances close examination of apparently poicilogonous polychaetes revealed the existence of multiple sibling species (Grassle and Grassle, 1976; Christie, 1982).

### *The study organism*

*Streblospio benedicti* (Spionidae) is a small (≤20 mm) infaunal polychaete that lives in the top few cm of muddy sediments and is a deposit and suspension feeder at the sediment-water interface. It is common in wetlands and estuaries throughout the Pacific, Gulf, and Atlantic coasts of North America and has also been reported from northern Europe, the Mediterranean Sea, the Black Sea, and Venezuela (Carlton, 1979).

*Streblospio benedicti* is best known as an opportunist which colonizes stressed or organically enriched sediments (Grassle and Grassle, 1974; Pearson and Rosenberg, 1978). *Streblospio* responds positively to structures on the mud surface such as artificial tubes (Dauer *et al.,* 1982), cages (Virnstein, 1977, 1978), settling containers (McCall, 1977; Levin, in press), or pits (Levin, in press) and has played a key role in studies of: meiofaunal-macrofaunal interactions in marshes (Bell and Coull, 1980; Watzin, 1983; and pers. comm.); predation in shallow infaunal communities (Quammen, 1981; Virnstein, 1977); competition among infauna (Levin, 1981, 1982a; R. Whitlatch, pers. comm.); and mesocosm dynamics (J. F. and J. P. Grassle, pers. comm., L. Watling, pers. comm.).

Though the reproductive characteristics of *S. benedicti* are important to the interpretations of all of these investigations, existing descriptions of development are spotty and conflicting. Larval development of *S. benedicti* has been described briefly by Campbell (1957) for Cape Cod (Massachusetts) populations and by Dean (1965) for Mystic River Estuary (Connecticut) populations; in both cases development was planktotrophic. Lecithotrophic development in west coast populations was discussed by Blake (1965) for Morro Bay, California and Levin (1982b) for Mission Bay, California. No previous descriptions of development are known for populations in the Gulf of Mexico.

## Materials and Methods

Sediment samples were collected by hand from 3 intertidal mudflats in California (Tijuana Slough, Dec. '82; Mission Bay, Nov. '82–April '83; and Elkhorn Slough, March '83), from tidal *Spartina* marshes in Texas (Big Slough, June and Oct. '83), Georgia (Sapelo Island, Nov. '83), and North Carolina (Tar Landing, Feb. and Oct. '83), and from shallow brackish water bays in Texas (Copano Bay, Oct. '83) and Florida (Sebastian River, March '83) (Fig. 1). Subtidal collections were also made in New Bedford Harbor, Massachusetts with a Van Veen grab (Oct.–Dec. '82) and from 6 m high cylindrical tanks at the Marine Experimental Research Laboratory (MERL) in Narragansett Bay, Rhode Island (Nov. '82–Aug. '83) with a pole-mounted core (5 $cm^2 \times 4$ cm depth). Salinities at all sites ranged from 28–34‰ except at Copano Bay (2‰) and Sabastian River (≈5‰).

Sediment samples were sieved through 300 or 500 $\mu$m screens and specimens of *Streblospio* were isolated for observation and initiation of laboratory cultures. Polychaetes were maintained at room temperature (20–23°C) in glass crystalizing dishes

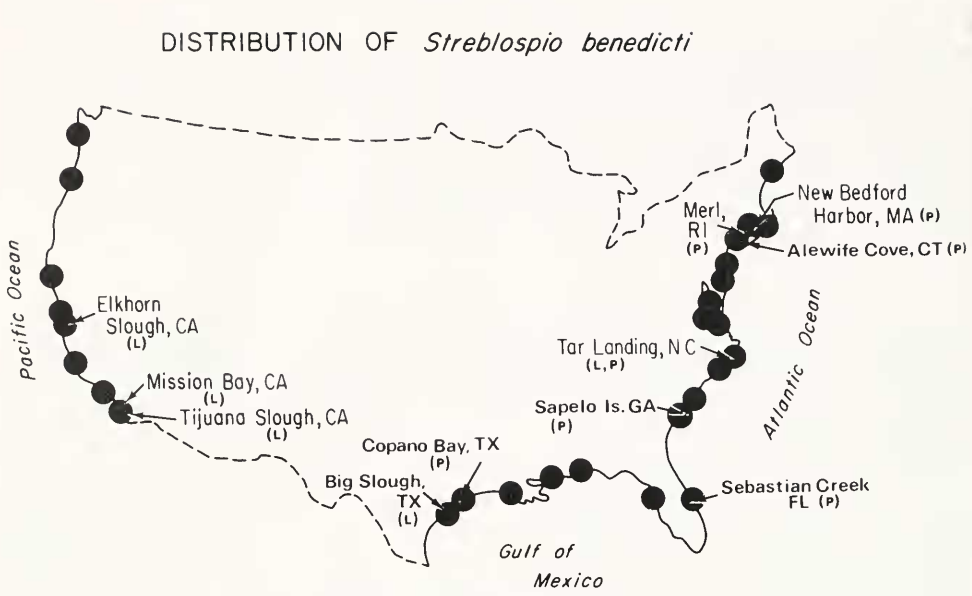



FIGURE 1. Distribution of *Streblospio benedicti* along the United States coastline, as given in the literature. Reproductive modes found at sampling sites in this study are labeled in parentheses ("L" = lecithotrophic, "P" = planktotrophic).

(8 cm diameter) containing fine sediments from Sippewissett Marsh in Falmouth, Massachusetts. Sediments (<1 mm diameter) were frozen (−30°C) to kill infauna, then mixed with sea water 5–7 days before addition to the polychaete cultures, to allow bacterial growth. The worms were given fresh sediment and mixed dinoflagellate cultures (*Prorocentrum, Perodinium, Gonyaulax, Gymnodinium*) every 4–5 days. Sea water and sediment were changed completely, approximately once a month.

Females brooding their young were isolated so that offspring from each parent could be followed separately. Duration of the planktonic period was determined by raising larvae individually in 13 × 100 mm glass test tubes at 20°C. The larvae were fed mixed dinoflagellate cultures, and sea water was not changed during the entire planktonic development. Fine sediment was added to the tube bottom in some vials to examine effects of substrate on development time or delay in settlement.

Reproductive features were measured on gravid females (relaxed with 1% $MgCl_2$) which had been freshly collected in the field or reared in the lab for 1–2 months. The characters quantified were: (1) body length (mm), (2) number of setigers, (3) maximum diameter of ova ($\mu$m), (4) number of ova per ovary, (5) first setiger involved in oogenesis, (6) number and position of brood pouches, (7) number of larvae brooded per pouch, and (8) brood size. Eggs in the coelom and larvae in brood pouches were observed through the transparent body wall of the female with a dissecting or compound microscope. Measurements were made using an ocular micrometer. In some instances early release of embryos in the female brood pouches was induced by prodding the (non-anesthetized) female. Embryos continued to develop normally, permitting the study of developmental stages which usually occur within brood structures. Larvae from populations in Mission Bay, Tijuana Slough, New Bedford Harbor, MERL, Big Slough, Copano Bay, and Sebastian River were observed and photographed at 1–2 day intervals following their release, using phase contrast optics (160×). The larval

traits recorded were (1) size at release, (2) mode of nutrition, (3) setation, (4) swimming behavior, (5) length of planktonic period, and (6) size at settlement.

Preliminary crossing experiments were conducted to evaluate the ability of individuals from different populations to interbreed and to test for evidence of hermaphroditism, sex reversals, parthenogenesis, or other forms of asexual reproduction. Nine sex-blind crosses were made by placing pairs of immature juveniles from Mission Bay and New England (New Bedford and MERL) populations in separate culture dishes. In addition, reciprocal matings were performed between virgin or isolated females and males from Big Slough and MERL, Big Slough and New Bedford, Big Slough and Copano Bay, and Tar Landing and MERL.

## Results

### *Female reproductive traits*

Oogenesis first occurs in setiger 7 but the exact segments involved varies among individuals and among populations. Oogenesis begins in more anterior segments in planktotrophic populations (setigers 7–11) than in lecithotrophic populations (setigers 12–14) (Table I). Ova develop within paired ovaries attached to genital blood vessels which extend into the coelomic space. The number of ova which develop in each segment also differs among individuals and among populations (Table I). In lecithotrophic populations 1–3 ($\bar{x} = 2.0$) ova may be observed through the body wall in each ovary. In planktotrophic populations 2–14 ($\bar{x} = 6.6$) ova develop in each ovary. The diameter of mature ova varies with trophic mode as well (Table I), ranging from 70 to 90 $\mu$m in planktotrophic populations and from 100 to 220 $\mu$m in lecithotrophic populations.

When ova are fully developed they move into posterior segments (presumably through the coelom), are fertilized by sperm stored in spermatophores, and enter coelomic brood pouches (Collier and Jones, 1967).

Larvae are brooded in paired dorso-lateral pouches (Fig. 2a) in all lecithotrophic and most planktotrophic populations observed (except those from Copano Bay and Sebastian River). Brood pouches can be present between setigers 17 and 45. They first appear between setigers 17 and 25 (Table I). The exact position varies with the size of the worm and, to some degree, among populations. Smaller worms have their brood pouches positioned more anteriorly than larger worms. The number of segments bearing pouches is positively correlated with the total number of setigers. For New Bedford $r = .67$, $P < .01$; for MERL $r = .87$, $P < .01$; for Tar Landing (Oct '83) $r = .65$, $P < .05$; and for Mission Bay $r = .83$, $P < .01$. Within each population larger worms, having more segments and more brood pouches, tend to produce greater numbers of larvae per brood than small individuals. Regressions of brood size on segment number are: for MERL $r = .72$, $P < .01$; for New Bedford $r = .57$, but $P > .05$; for Tar Landing in Oct. '83 $r = .70$, $P < .05$; for Big Slough $r = .38$, $P < .05$; and for Mission Bay $r = .42$, but $P > .05$. The slope of the regression line ranges from 6.7 to 7.9 in planktotrophic populations and from 0.71 to 2.60 in lecithotrophic populations.

The number of larvae brooded per pouch and the number of larvae produced per brood differ considerably in planktotrophic and lecithotrophic populations, independent of adult size (Table I, Fig. 3). Lecithotrophic females generally brood 1–2 larvae per pouch, in 5–16 paired pouches (Table I), to yield brood sizes of 8–59 (Fig. 3). Mean brood sizes for lecithotrophic populations are: 32 for Mission Bay ($n = 18$); 14 for Big Slough ($n = 28$); and 20 for Tar Landing Oct. '83 ($n = 9$). Over 95% of brood pouches bearing lecithotrophic embryos contain only 1 or 2 larvae

TABLE I

*Female reproductive traits*

| | Planktotrophic populations | | | | | Lecithotrophic populations | | | | Analysis of variance |
|---|---|---|---|---|---|---|---|---|---|---|
| | NEW BEDFORD HARBOR, MA | MERL, RI | TAR LANDING, NC 2/83 | SEBASTIAN R., FL. | COPANO BAY, TX | MISSION BAY, CA | TIJUANA SLOUGH, CA | BIG SLOUGH, TX | TAR LANDING, NC 10/83 | F |
| Total # of Segments (mature females) | | | | | | | | | | |
| $\bar{x}$ | 54.8 | 43.4 | 56.0 | 69.0 | 44.5 | 49.8 | 49.4 | 44.1 | 41.3 | $F_{8,191=36.39}$* |
| S.D. | 4.7 | 5.6 | 2.8 | 6.6 | 3.8 | 3.3 | 1.7 | 4.8 | 2.8 | |
| n | 52 | 48 | 5 | 3 | 6 | 30 | 8 | 39 | 11 | |
| First Setiger Bearing Ova | | | | | | | | | | |
| $\bar{x}$ | 11.5 | 10.2 | 11.1 | 11.3 | 7.8 | 13.5 | 14.0 | 12.6 | 12.1 | $F_{8,187=20.13}$* |
| S.D. | 1.7 | 0.6 | 1.1 | 4.7 | 0.4 | 2.3 | 1.6 | 1.3 | 1.3 | |
| n | 46 | 50 | 7 | 4 | 6 | 33 | 10 | 31 | 9 | |
| Ova/Ovary | | | | | | | | | | |
| $\bar{x}$ | 6.3 | 5.3 | 8.0 | 7.0 | 6.3 | 2.0 | 2.1 | 1.9 | 1.9 | $F_{8,166=33.78}$* |
| S.D. | 2.0 | 2.0 | 2.2 | 2.6 | 1.5 | 0.6 | 0.3 | 0.9 | 0.6 | |
| n | 35 | 53 | 6 | 4 | 6 | 25 | 9 | 29 | 8 | |
| Ovum Diameter (all present) | | | | | | | | | | |
| $\bar{x}$ | 69.7 | 59.1 | 62.9 | 68.0 | 56.7 | 115 | 152 | 140 | 152 | $F_{8,168=21.89}$* |
| S.D. | 24.7 | 25.3 | 25.0 | 29.3 | 13.7 | 37 | 43 | 52 | 70 | |
| n | 39 | 54 | 7 | 4 | 6 | 28 | 8 | 22 | 9 | |
| 1st Setiger Bearing Brood Pouch | | | | | | | | | | |
| $\bar{x}$ | 22.9 | 19.7 | 23.8 | 24.0 | 18.6 | 22.9 | 22.9 | 20.1 | 19.5 | $F_{8,198=34.94}$* |
| S.D. | 1.6 | 1.5 | 1.1 | 2.6 | 0.5 | 1.0 | 1.2 | 1.3 | 1.9 | |
| n | 52 | 49 | 5 | 3 | 5 | 34 | 9 | 39 | 11 | |
| Number of Brood Pouches | | | | | | | | | | |
| $\bar{x}$ | 12.9 | 9.2 | 11.0 | 16.7 | 9.0 | 9.2 | 8.4 | 6.8 | 6.7 | $F_{8,196=19.56}$* |
| S.D. | 3.3 | 2.7 | 1.3 | 1.5 | 2.7 | 2.0 | 1.5 | 1.8 | 1.8 | |
| n | 52 | 48 | 6 | 3 | 5 | 32 | 9 | 39 | 11 | |
| Number of Larvae Per Pouch | | | | | | | | | | |
| $\bar{x}$ | 8.7 | 6.6 | 8.0 | — | — | 2.7 | 2.0 | 1.9 | 1.9 | $F_{6,90=51.72}$* |
| S.D. | 2.4 | 2.3 | 0 | — | — | 1.1 | 0.0 | 0.6 | 0.5 | |
| n | 13 | 19 | 3 | — | — | 18 | 2 | 31 | 11 | |
| Brood Size | | | | | | | | | | |
| $\bar{x}$ | 175.4 | 104.6 | 141.8 | 195.0 | 111.0 | 31.7 | — | 15.3 | 19.8 | $F_{7,98=36.68}$* |
| S.D. | 47.2 | 59.0 | 45.2 | 113.1 | 31.6 | 10.7 | — | 7.5 | 10.6 | |
| n | 10 | 29 | 4 | 2 | 6 | 18 | — | 28 | 9 | |

* $P < .0001$.

(Fig. 2a, Table I). Occasionally lecithotrophic individuals collected in the field will brood up to three larvae per pouch, and one Mission Bay specimen reared in the laboratory was found with six lecithotrophic larvae in a single pouch. Planktotrophic females brood 4–14 larvae per pouch (Fig. 2b) in 5–23 paired pouches, releasing broods of 25–548 larvae (Fig. 3, Table I). Mean brood sizes are 175 (n = 10) for New Bedford; 105 (n = 26) for MERL (control tanks); and 142 (n = 5) for Tar Landing Feb. '83. A maximum brood size of 548 was observed for a *Streblospio* female collected from a MERL tank enriched at 8 × normal Narragansett Bay nutrient levels.

Planktotrophic development in females from Copano Bay and Sebastian River appears not to involve brood pouches. Embryos are brooded inside the parental tube against the dorsal surface of the female. They are partially enclosed by branchiae (vascularized lobes) present on segments between setigers 18 and 41 (Fig. 2c) and appear to adhere to the female. When she moves inside the tube the embryos are transported with her. The vascularized branchiae are similar in size and appearance to the large blood vessels embedded dorsally in the brood pouches present in other populations, and occur on those setigers which would otherwise be expected to support brood pouches. When the female leaves her tube, embryos or larvae are automatically released. Larvae brooded in pouches (in other populations) are normally retained within them, even outside the tube, unless the female is disturbed. Total brood sizes in these pouchless populations are comparable to those in pouch-brooding planktotrophic forms (Table I).

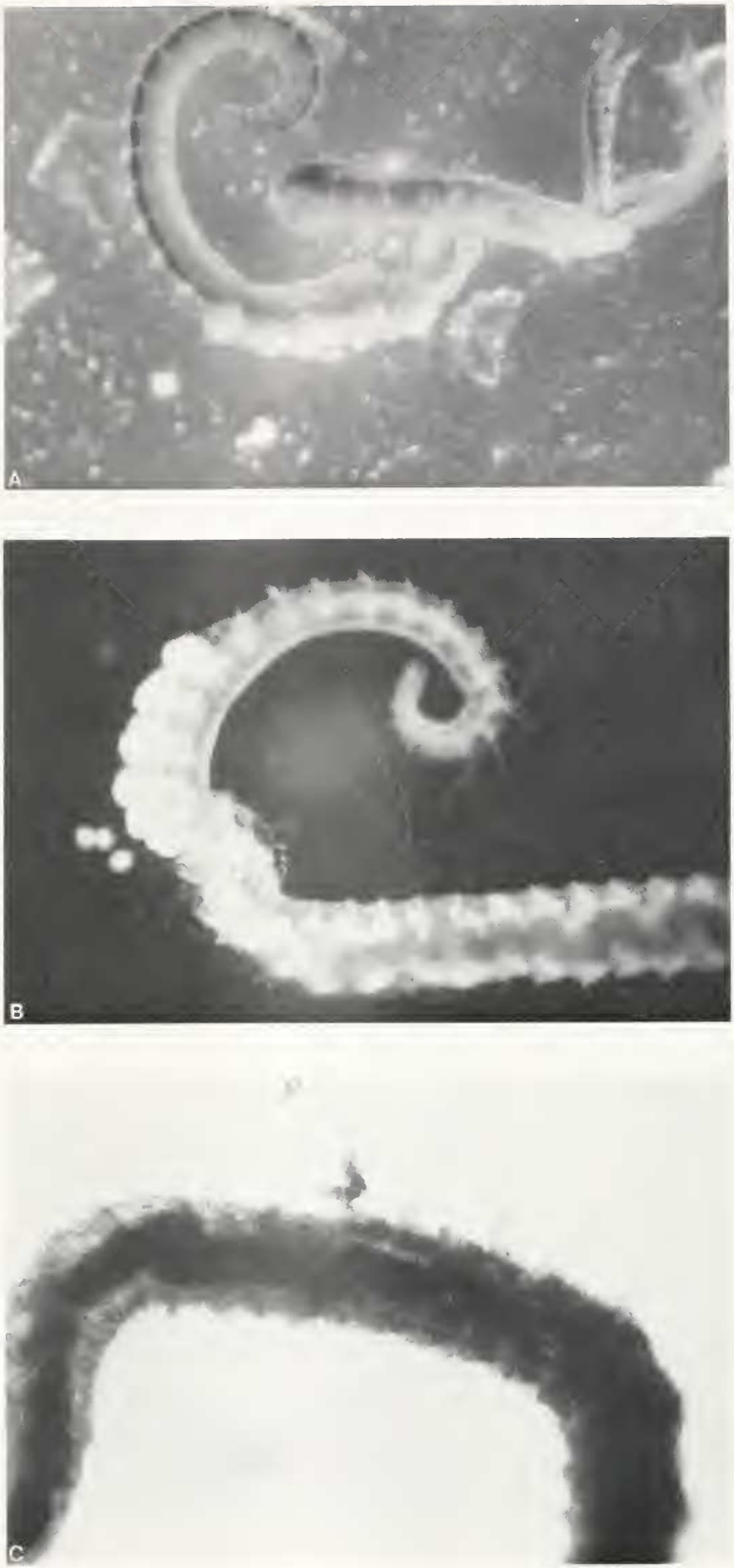
One Way Analysis of Variance of female reproductive traits yielded significant differences among populations for all characters tested (Table I). Student-Neuman-Keuls *a posteriori* tests documented distinct grouping of populations by trophic mode for the following traits: 1st ovigerous setiger, number of ova/ovary, ovum diameter, number of larvae per brood pouch, and brood size (Table II). In lecithotrophic populations oogenesis begins more posteriorly, produces fewer ova of larger diameter, and results in considerably smaller brood sizes than in planktotrophic populations.

### *Larval development*

Lecithotrophic development was observed at all collection sites on the Pacific Coast, in the Gulf of Mexico at Big Slough, and on the Atlantic Coast at Tar Landing in October 1983. Planktotrophy was observed in specimens from all Atlantic Coast study sites including Tar Landing in February 1983 and from Copano Bay. Only in Tar Landing were both forms of larval development observed at a single site and these observations (of planktotrophy and lecithotrophy) were separated by ≈9 months. Later collections, made in early 1984, indicate that both planktotrophic and lecithotrophic forms are present at Tar Landing during January and February.

Laboratory cultures initiated from each collection bred true to the 'wild' type. Forms which were planktotrophic at the time of collection remained so and produced subsequent generations which were also planktotrophic. The same was true of lecithotrophic populations. Planktotrophic populations have been followed in the laboratory for up to 3 generations (≈3 mo/generation); and lecithotrophic populations for up to 4 generations (≈2–3 mo/generation).

Lecithotrophic development in *S. benedicti* is characterized by large ova, whose massive yolky embryos develop entirely within the brood pouch (Table III). Within 3 days of fertilization the trochophore is 300–340 μm in length. Segments are added at a rate of 1 or 2 per day and by day 7 or 8 (at 20°C) a fully developed larva (≈550–650 μm length) is released (Fig. 4A, B, and C). Late stage larvae may develop


A
B
C

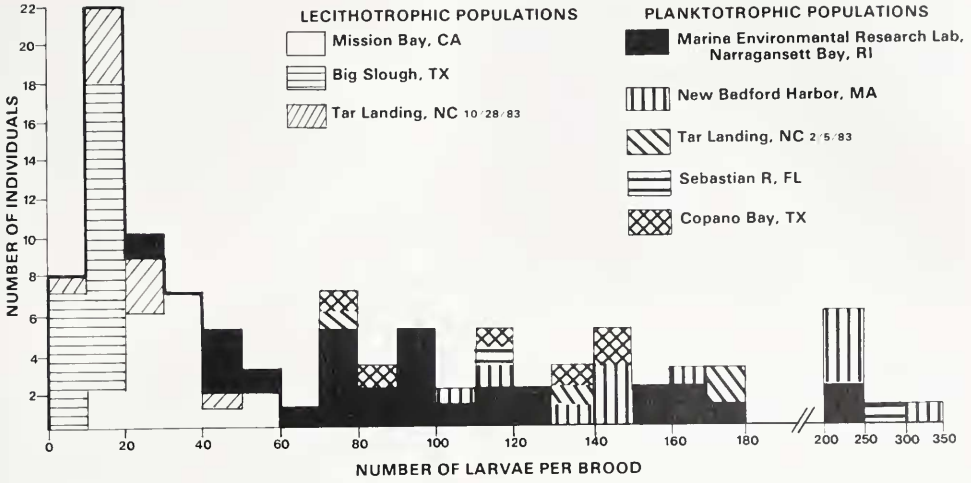



FIGURE 3. Observed distribution of brood sizes are shown in three lecithotrophic and five planktotrophic *Streblospio benedicti* populations.

adult setae (capillary setae and hooded hooks), but at no time do they exhibit the long swimming setae characteristic of many spionid larvae.

Lecithotrophic *S. benedicti* larvae are competent to settle at 9–12 setigers and generally settle at the time of their release. They may recruit without ever entering the water column. However, in the absence of suitable substrate, larvae may remain planktonic up to 7 days (Fig. 5). Following release from the brood pouch into the water column, larvae appear to derive nutrition from original yolk supplies. Stored yolk was observed to sustain larvae for approximately one week without external sources of food.

Planktotrophic *S. benedicti* larvae differ most noticeably from lecithotrophic forms in the presence of long "swimming" setae, a decreased yolk supply, a functional gut early in development, and a longer planktonic development (Table III). Within 2–3 days after fertilization (at 20°C), small ova develop into larvae with a single set of long serrated setae. Development usually proceeds inside the brood pouch to a 4-setiger stage within 24 hours and to 5–7 setigers within 2–3 more days (Fig. 4D, E, and F). Long serrated setae develop on each segment as they are added. The larvae have fully formed guts at the 4-setiger stage ($\approx$250–300 $\mu$m) and if released they begin planktonic feeding. Strong swimming ability and positive phototaxis is evident throughout the planktonic phase. Larval release normally takes place at 5–7 setigers (300–350 $\mu$m). Copano Bay and Sebastian River (pouchless) females have not been observed to brood beyond the 3 setiger stage. In other respects development of the pouched and pouchless planktotrophic forms appears to be identical.

Planktotrophic larvae settle within 2–3 weeks of their release at $\approx$9 setigers, though in the absence of suitable substrate the planktonic period may exceed 35 days

FIGURE 2. A. *S. benedicti* brood pouches bearing lecithotrophic embryos. Female collected from Big Slough, Texas, October, 1983. B. *S. benedicti* brood pouches bearing planktotrophic embryos. Female collected from New Bedford Harbor, Massachusetts, February, 1983. C. Brood structures on a *S. benedicti* female from Copano Bay, Texas, October, 1983. Note the absence of brood pouches. Vascularized branchiae appear in their place.

TABLE II

*Reproductive similarities and differences among* S. benedicti *populations*

| | |
|---|---|
| LENGTH | TL(F) SR NBH TJS MB BS TL(O) CB MERL |
| NUMBER OF SETIGERS | SR TL(F) NBH TJS MB CB BS MERL TL(O) |
| FIRST OVIGEROUS SETIGER | TJS MB BS TL(O) NBH SR TL(F) MERL CB |
| NUMBER OF OVA PER OVARY | TL(F) SR CB NBH MERL TJS MB BS TL(O) |
| OVUM DIAMETER | TJS TL(O) BS MB NBH SR TL(F) MERL CB |
| FIRST SETIGER BEARING POUCHES | SR TL(F) MB TJS NBH BS MERL TL(O) CB |
| NUMBER OF POUCHES | SR NBH TL(F) MERL MB CB TJS BS TL(O) |
| NUMBER OF LARVAE PER POUCH | NBH TL(F) MERL MB TJS TL(O) BS |
| BROOD SIZE | SR NBH TL(F) CB MERL MB TL(O) BS |

Abbreviations represent the following populations:

NBH = New Bedford Harbor, Massachusetts

MERL = Marine Experimental Research Laboratory, Narragansett Bay, Rhode Island

TL(O) = Tar Landing, North Carolina, October 1983 Collection

TL(F) = Tar Landing, North Carolina, February 1983 Collection

SR = Sebastian R, Florida

BS = Big Slough, Texas

CB = Copano Bay, Texas

TJS = Tijuana Slough, California

MB = Mission Bay, California

Results are based on Student-Neuman-Keuls *a posteriori* tests performed for each trait following One Way Analysis of Variance. Populations connected by lines are not significantly different. Heavy lines indicate lecithotrophic populations, light lines indicate planktotrophic populations. (See Table I for data.)

TABLE III

*Contrasting patterns of larval development in* Streblospio benedicti

| | Planktotrophic Populations | Lecithotrophic Populations |
|---|---|---|
| # LARVAE BROODED/BROOD POUCH | 4–14 | 1–2, occasionally 3 |
| BROOD SIZE | $\bar{x}$ = 130, s = 65 | $\bar{x}$ = 20, s = 12 |
| DEVELOPMENT TIME TO RELEASE (20°C) | $\approx$7 days | $\approx$7 days |
| LARVAL STAGE AT RELEASE | 3–7 setigers | 9–12 setigers |
| LARVAL SIZE AT RELEASE | 200–300 $\mu$m | 500–650 $\mu$m |
| PLANKTONIC FEEDING | begins at 4 setigers | none |
| SWIMMING SETAE | present | reduced or absent |
| DURATION IN THE PLANKTON (20°C) | 7–45 days | $\leq$7 days |
| SIZE AT SETTLEMENT | 450–550 $\mu$m | 550–650 $\mu$m |

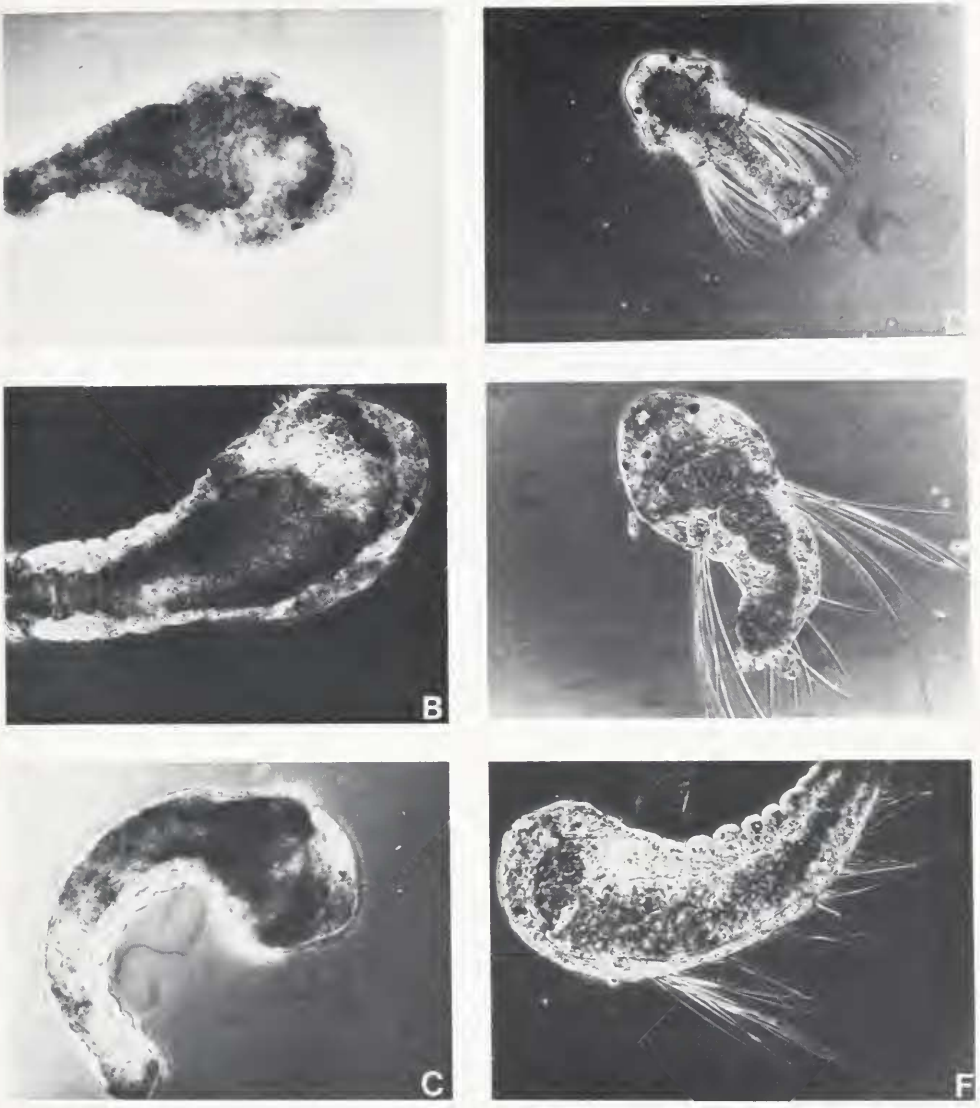



FIGURE 4. *Streblospio benedicti* larval stages. Note absence of swimming setae in lecithotrophic Pacific forms (A, B, C) and presence in planktotrophic Atlantic forms (D, E, F). A. Pacific Coast larva from a female collected in Tijuana Slough, California and cultured in the laboratory for one month. Shown four days after fertilization, 330 $\mu$m, four segments. B. Pacific Coast larva from the same brood (Tijuana Slough, California). Shown six days after fertilization, 535 $\mu$m, eight segments. C. Pacific Coast larva from the same brood (Tijuana Slough, California). Shown seven days after fertilization, 600 $\mu$m, nine segments. This is the stage at which release from the brood pouch normally occurs and at which the larva is competent to settle. D. Atlantic coast larva from a female collected in New Bedford Harbor, Massachusetts and cultured in the laboratory for one month. Shown three days after fertilization, 280 $\mu$m, one setiger. E. Atlantic coast larva from a female collected in MERL, Rhode Island. Shown five days after fertilization, 350 $\mu$m, five setigers. F. Atlantic coast larva from a female collected in New Bedford Harbor, Massachusetts. Shown 22 days after release, 500 $\mu$m, nine setigers.

(Fig. 5). The duration of the planktonic phase, particularly of the competent period (during which a larva is capable of settling), is highly variable in planktotrophic *S. benedicti,* even for larvae from a single brood. However, the probability of settlement

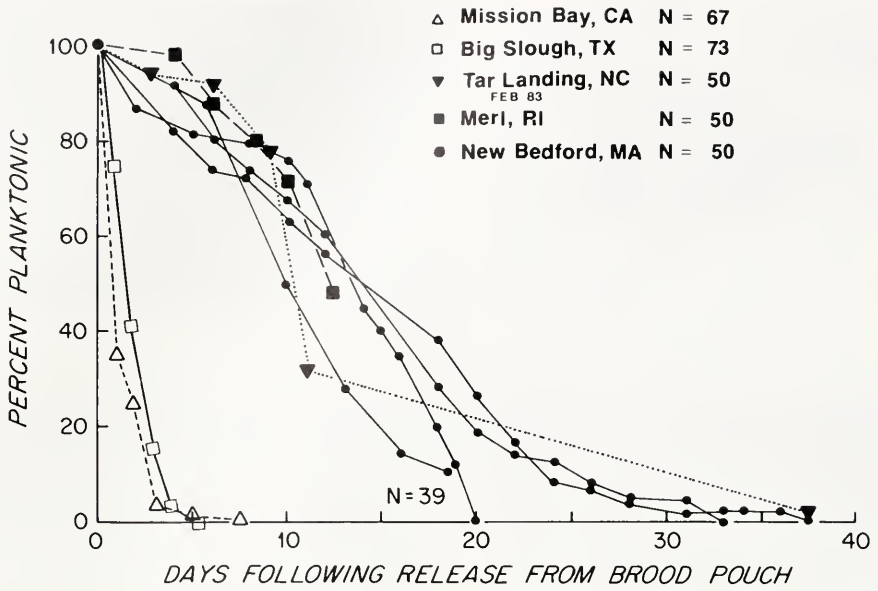



FIGURE 5. Planktonic period of *Streblospio benedicti* larvae raised individually in glass tubes without substrate at 20°C. Larvae were fed mixed phytoplankton cultures. Each line represents survivorship of individuals from a single brood or from pooled broods (Mission Bay, California, 3 broods and Big Slough, Texas, 7 broods). Loss from the plankton is taken to occur when larvae first permanently settle onto the tube bottom.

at any time after release is similar for larvae from different females and even from different populations (Fig. 5).

*Interbreeding potential*

Sex-blind pairings demonstrated that *S. benedicti* is a dioecious species which, at least under laboratory conditions, does not reproduce hermaphroditically or asexually. Analysis of nine pairings between Mission Bay juveniles and New England (MERL or New Bedford) juveniles after 2 months in culture revealed 4 male/female pairs, 4 female/female pairs, and 1 male/male pair. None of the single sex pairs showed any evidence of reproduction though all individuals contained ripe gametes. All male/female pairs had reproduced successfully, two producing lecithotrophic larvae by Mission Bay females and 2 producing planktotrophic larvae by New England females.

The $F_1$ larvae from crosses in both directions settled and successfully produced $F_2$ larvae by interbreeding among themselves. Additional inter-development mode reciprocal matings were conducted successfully between individuals from Big Slough × MERL, -× New Bedford, and -× Copano Bay, and between Tar Landing (lecithotrophs) × MERL. Results of these crosses will be presented in a later paper. They are mentioned here to demonstrate the interfertility of *S. benedicti* populations.

## DISCUSSION

The observation of both planktotrophic and lecithotrophic development in *Streblospio benedicti* raises numerous mechanistic and evolutionary questions. The function of oogenic and vitellogenic processes, the relative roles of environment *versus*

genotype, and the ecologic, taxonomic, and evolutionary consequences of the observed life history differences, have yet to be fully clarified.

*Reproductive plasticity*

The apparent plasticity of *S. benedicti* may be an evolutionary phenomenon in that different strains or subspecies may have differentiated with respect to mode of reproduction. An ecological alternative is that environmental cues trigger changes in oogenesis and vitellogenesis which produce the observed reproductive patterns. Eckelbarger (1980) reports that in *S. benedicti* there is a heterosynthetic uptake of blood pigment molecules from the blood vessel lumen in addition to autosynthetic vitellogenic processes. The ability to derive yolk precursors from extraovarian sources might allow *S. benedicti* to adjust ovum volume and number. Enrichment studies involving *S. benedicti* indicate that planktotrophic individuals can double or triple brood size in response to an increase in available organic matter (Levin, unpub.).

It is not known whether a single *S. benedicti* individual can switch reproductive modes and produce both planktotrophic and lecithotrophic larvae. This behavior was never observed in the laboratory. All 'wild' (field collected) specimens reared in the laboratory ($\approx$50 lines), and their progeny, exhibited reproductive characters identical to those of the field population. This observed continuity, and the occurrence of intermediate larval traits in $F_2$ progeny of $F_1$ hybrids resulting from inter-development mode crosses (Levin, in prep.), suggest that there is a strong genetic component to most of the reproductive characters monitored, including egg size, egg number, setation, and trophic mode.

The observation of both reproductive modes at Tar Landing (planktotrophy in Feb. '83 and lecithotrophy in Oct. '83) does suggest that individuals are capable of switching development mode. Alternatively, individuals with different genotypes within a single population may reproduce at different times, producing the observed pattern. The planktotrophic population sampled in February could have been replaced completely by recruitment of lecithotrophic individuals prior to the October sampling. The life span of *S. benedicti* individuals reared in the laboratory at 20°C (in the absence of predation) appears to be 6–12 months. However, generation times are only 2–3 months and individuals begin to lose reproductive vigor between 6 and 8 months of age.

The initial observation of dramatic life history differences among *Streblospio benedicti* populations suggested possible systematic differences between these forms. However, cross-breeding experiments demonstrate that the planktotrophic and lecithotrophic forms of *S. benedicti* are not reproductively isolated and thus do not merit species status. $F_1$ progeny resulting from crosses between the two forms are fertile as are subsequent generations (Levin, in prep.).

*Ecological considerations*

The reproductive variability of *S. benedicti* is probably partly responsible for the success of this species in North American bays and wetlands. This variation may have important implications for the population ecology of the species. Brood size, which can be ten or twenty times greater in planktotrophic than lecithotrophic *S. benedicti* (Fig. 3), will influence larval availability and potential rates of population increase (r). In both planktotrophic and lecithotrophic populations females produce multiple broods and larvae can rapidly colonize disturbed areas (Grassle and Grassle, 1974; Levin, in press; McCall, 1977; Oliver, pers. comm.; Quammen, 1981; Whitlatch, pers. comm.). However, the observed differences in larval planktonic period suggest

that planktotrophic *S. benedicti* larvae possess much greater powers of dispersal. This conclusion is supported by the known occurrence of larvae in the plankton. In California bays, *S. benedicti* larvae, which are all lecithotrophic, are rarely collected in plankton tows. This was observed even when *S. benedicti* was the numerically dominant species in bottom sediments (Levin, in press; Blake, pers. comm; Nichols, pers. comm.). The reduced dispersal capability of lecithotrophic *S. benedicti* larvae is characteristic of many Pacific coast infaunal species (annelids, molluscs, and crustaceans) inhabiting back-bay environments (Levin, in press).

In contrast to the Pacific coast situation, planktotrophic *S. benedicti* larvae are often the most abundant component of the summer meroplankton in Atlantic coast estuaries (Dean, 1965; Simon and Brander, 1966). The ability of planktotrophic larvae to prolong planktonic development may improve chances of finding a suitable site for settlement under certain conditions. Planktotrophic *Streblospio,* in addition to a longer planktonic development, have stronger swimming abilities, faster speed, and more maneuverability (pers. obs. using videotapes) than lecithotrophic forms, and can feed in the water column during much of the development period. Thus, planktotrophic *S. benedicti* larvae appear to possess excellent dispersal abilities and probably exercise considerable powers of habitat selection.

In lecithotrophic forms, parental females may be more important than larvae in selection of offspring habitat. Studies in Mission Bay, California demonstrated that brooding females actively colonized disturbed sediments. Release of young followed by minimal dispersal resulted in rapid local increases in population size following colonization by only a few females (Levin, in press). Observations of high *S. benedicti* densities in artificial settling trays have led to the suggestion of *in situ* reproduction on the Atlantic coast as well (McCall, 1977; Whitlatch, pers. comm.) but it is not clear whether these studies involved planktotrophic or lecithotrophic forms.

I suggest from these findings that marine ecologists need to look carefully at the life history traits of community members. We should not assume that life history traits reported in the literature for a particular population will necessarily be accurate for different populations.

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